Origins and Setting: Mammal Quaternary Palaeontology in the Eastern Highlands of New South Wales

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Fossil mammal faunas found in the early years of Australian cave exploration were primarily regarded as a source of information on the diversity and anatomy of the extinct megafauna although they certainly played an important part in shaping the awareness that led to ideas of evolutionary biogeography. Thomas Mitchell, who had a leading role in their early discovery, also suggested correlations of the Wellington deposits with climatic fluctuations, with sea levels, with lunette formation and with the development of landscape. Later palaeoclimatic speculations by Owen and Darwin were based on faunal analogy. At that time, it was not possible to extend these speculations further.

Interest in finding fossil ancestors led to some Pleistocene forms being regarded as ancestral to modern taxa but it was generally agreed that, as "Ice Age" equivalents, they only illustrated the demise of megafauna as did cave faunas in Europe and South America.

Now, because of extensive palaeoclimatic information derived from a wide range of disciplines, and realization that the caves of eastern Australia contain deposits extending back into the Tertiary, and the recognition that by far the greater part of the characteristic modern Australian marsupial radiation (and much of the murid radiation) is arid adapted, it seems likely that the caves have the potential to illustrate the spectacular and rapid Australian radiation after the loss of most of the rainforests.

The topographic and ecological diversity of eastern Australia also highlights the sensitivity of the Eastern Highland cave faunas as indicators of faunistic and climatic change, but currently, very few reliably dated mammal-bearing deposits are known in the highlands. However, studies made recently of both cave and fluviatile deposits indicate the occurrence of faunal change and turnover during the Pleistocene, and well before the last glacial maximum, followed by progressive faunal depauperization. The loss of megafauna occurred before climatic amelioration following the glacial maximum. The reason is not apparent.

Fossil faunas reveal unexpected associations that indicate that our knowledge of the evolution of physiological and behavioural responsiveness of animal species to environmental factors (such as climate, soils, and topography) may not be as closely correlated with morphological evolution as is required to enable palaeofaunal distributions to be used as the basis of faunal predictions of the effects of global warming. Alternatively, it may be that distributions that currently seem to be discordant are, in fact, the product of imprecise morphotaxonomy as is suggested by recent work on *Burramys*.

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KEYWORDS: Cave fossils, megafauna, Mitchell, Owen, paleoclimatology, Quaternary

ORIGINS: DISCOVERY, SCIENCE AND COMMITMENT

Although there is evidence that other caves were found in the years immediately before the caves in the Wellington Valley, none was reported as being fossiliferous and if one were to designate any place in Australia as being the founder site of Australian vertebrate palaeontology, we have no doubt that it would be the caves in which this opening address of our symposium is being given — the great Cathedral Cave (and the nearby "Breccia Cavern" = Mitchell's Cave, see cover), at Wellington (Lane and Richards 1963, Dawson 1985).

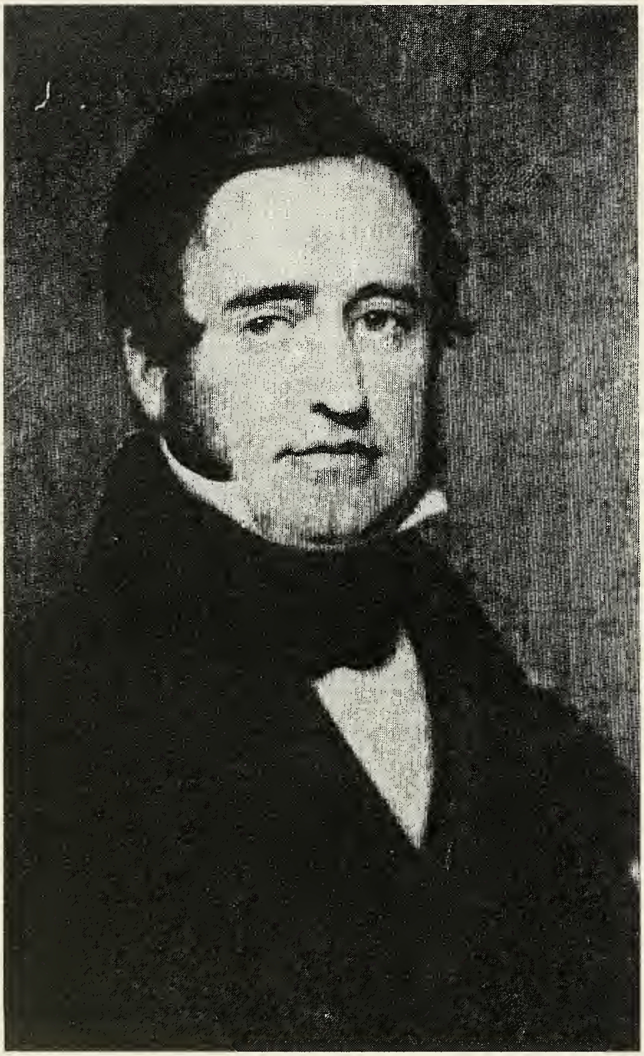

Figure 1. George Ranken: settler and magistrate of Bathurst, NSW. Discoverer of the Breccia Cave: Mitchell's Cave, Wellington. Reproduced by permission of Mrs M. Suttor.

The discovery was first announced, in Sydney, on the 25th May 1830 in a letter and editorial in the *Sydney Gazette and New South Wales Advertiser,* that Mr George Ranken (Fig. 1), colonist and magistrate, had found a deposit of fossil bones in these caves (Anon 1830a, b). A few months later the discovery was made known to the scientific world in the *Edinburgh New Philosophical Journal* by Colonel Patrick Lindesay, who was then stationed with the 39th Regiment in New South Wales (Lindesay 1830) and *de facto* Lieutenant Governor. Lindesay was an active naturalist and promoter of natural history. Educated at the University of Edinburgh, he was a friend and correspondent of the editor of the journal, Professor Robert Jameson (Regius Professor of Natural History at the University of Edinburgh) (Wittell 1954, Chisholm 1967).

Palaeontological interpretations accompanied the announcement in the *Sydney Gazette*. The correspondent observed that the deposit seemed to contain extinct forms only, and speculated on the aetiology of the deposit and its relation to the universal Deluge (see below). Ranken had made a small collection and, as indicated in the *Sydney Gazette*, it was sent abroad for examination. Lindesay sent it to Jameson by the Rev John Dunmore Lang who travelled to Britain in 1830 (Anon. [Jameson] 1831a, Pentland in Anon. [Jameson] 1831b, Baker 1967). From the collection, Jameson and a colleague, Dr Adam (Jameson 1831), identified wombat and kangaroo teeth and an animal "larger than any of the living species in the Australian world" which appeared to resemble the radius of a specimen of hippopotamus in the Edinburgh College Museum. Jameson then sent the bones to William Clift of the College of Surgeons, London, who added the Tasmanian devil to Jameson and Adam's list. Clift agreed that the large bone bore a resemblance to the radius of a hippopotamus and commented that 'It does not belong to the elephant ...' (Clift 1831, p. 394).

From Clift, the much-travelled bones went to Cuvier in Paris and were reported on there by Cuvier's colleague, Pentland, who provided a new list of identifications. As well as the marsupials identified previously (to which Pentland added a species of rat kangaroo and a wallaby one third larger than the kangaroo), he listed "Elephant, one species" (Pentland in Anon. [Jameson] 1831b). He later (Pentland 1832) considered this bore a closer resemblance to the fossil elephant "common in the valley of the Arno" than to either the African or Indian elephant. Ranken's collection then returned to Edinburgh and was deposited in the Edinburgh College Museum (now the Royal Scottish Museum, Andrews 1982, p. 56). In the three years from its discovery, study in Edinburgh, London and Paris had revealed the occurrence of an extinct fauna in Australia of mammals belonging to the same groups as the modern fauna, and which, like those of other continents, included gigantic forms (the 'hippopotamus/elephant' seems now to have been a gigantic Australian dromornithid, Rich 1985, p.191). Its study had made a significant contribution to the debate over the universality of the Deluge and to the beginnings of a historical perspective in biogeography.

Although Ranken's collection was an important beginning, it was the very lively interest and energy of his friend, Major Thomas Mitchell, the Surveyor General of New South Wales (Fig. 2), his careful field observations, his published geological descriptions and inferences (Mitchell 1831a, b), the wide public reached through his book of explorations in New South Wales (1838) and, most importantly, from 1837 onwards his relationship with Richard Owen (Fig. 3) at the Royal College of Surgeons in London, that were instrumental in developing the scientific potential of the caves and their bones.

Like Ranken, Mitchell had also made and sent a collection of bones from Wellington Caves to Britain in 1831 (he also sent a second collection to Cuvier in Paris (Pentland 1833, Foster 1936)). Mitchell donated the collection to the Geological Society of London (Anon. 1831) of which he was a Fellow. It was an extensive collection consisting of three large boxes of bones accompanied by ten plans and drawings and a "report of 36 pages" (Ranken 1916, p.23). The report was published in abridged form (Mitchell 1831b) and, later, more extensively in his *Three Expeditions...* (Mitchell 1838). The contribution by Richard Owen on the specimens in the latter work was to provide the first detailed anatomical descriptions and naming of the fossils. Moreover, the research on this collection generated a lasting commitment to the study of Australian fossil mammals by the greatest anatomist of the time — to be followed by succeeding generations both in Britain and Australia.

The "philosophical" setting in which the discovery of Wellington Caves and its fossils took place is important for an understanding of what, as well as sheer love of exploration, encouraged people like Mitchell to go out of their way to spend time and energy not only on exploring caves for fossils but, more importantly, to take considerable trouble to preserve and pass on their finds to experts eager to interpret them. In the eye of the edu-

Figure 2. Major Thomas Mitchell: Surveyor General of New South Wales. First describer of the fossil-bearing Wellington Cave deposits. Reproduced by permission of the Mitchell Library, State Library of NSW.

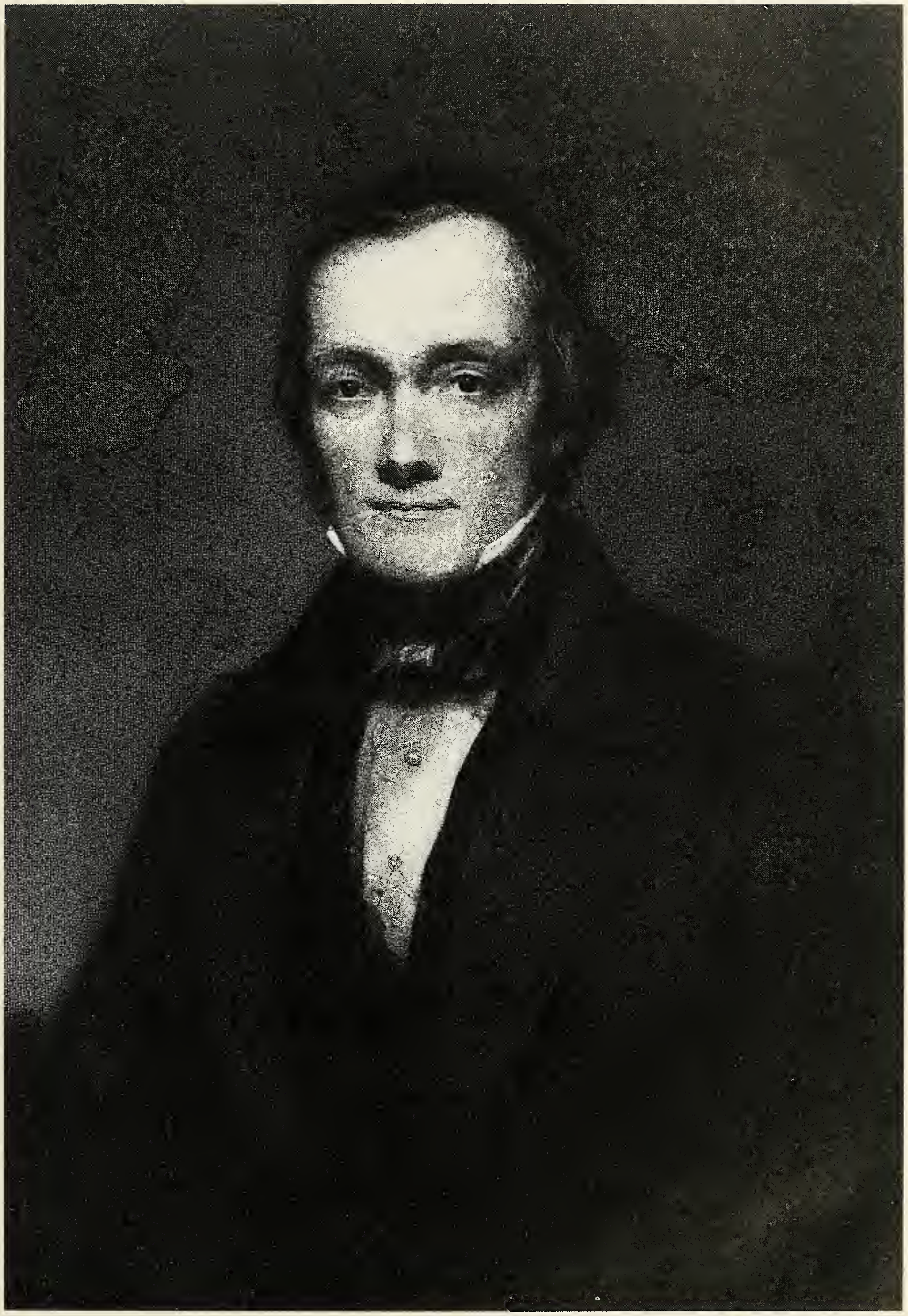

Figure 3. Professor Richard Owen, Hunterian Professor, Royal College of Surgeons, London. c 1844 from a mezzotint by W. Walker from a portrait by H.W. Pickersgill. Reproduced by permission of the Trustees of the Wellcome Institute: from the collection of the Wellcome Institute Library, London (no. 2197.2).

cated public cave fossils were the stuff of controversy at the time and people in New South Wales, like George Ranken and Thomas Mitchell, were very aware of divergent interpretations that were being placed on them in Europe (Ranken 1916, Foster 1936, Rudwick 1972, Dawson 1985). Fossils held an interest that extended well beyond scientific circles because they were the centre of a widening public awareness that biblical literalism was under renewed challenge as the result of the new discoveries of geology.

Although in scientific and theological circles the challenge to the inerrancy of the Scriptures had been an ongoing debate from the time of Copernicus (see Brooke 1991) and was widely accepted by intellectuals on scientific and other grounds (both textual and historical), it was elevated into public consciousness by current findings in geology (see Rudwick 1972). More particularly, discoveries in palaeontology, and especially of extinct mammal faunas in European and British caves, caught the public imagination. Discoveries were effectively publicised by the Rev Dr Buckland, Reader in Geology at Oxford, who, as a geologist–theologian was both influential and a popular public speaker. Initially, in opposition to such distinguished scientists as Linneaus and Cuvier, he interpreted the discoveries as proofs of the Noachian flood (Buckland 1824: 221–228), but this view was contested by contemporary geologists (and especially by his influential pupil Charles Lyell 1830–33). Within a decade, in his second major work, Buckland stated that the facts now contradicted his earlier view (Buckland 1836: 94–5). He went further and, as a senior churchman, presented an unmistakable challenge to literalist interpretation of Scripture in favour of what the rocks reveal of the historical past (including evidence of design). Buckland said

> "If the suggestions I shall venture to propose require some modification of the most commonly received and popular interpretation of the Mosaic narrative, this admission neither involves any impeachment of the authenticity of the text, nor of the judgement of those who have formerly interpreted it otherwise, in the absence of information as to facts which have but recently been brought to light; and if, in this respect, geology should seem to require some little concession from the literal interpreter of scripture, it may fairly be held to afford ample compensation for this demand, by the large additions it has made to the evidences of natural religion, in a department where revelation was not designed to give information.[1]
>
> The disappointment of those who look for a detailed account of geological phenomena in the Bible, rests on a gratuitous expectation of finding therein historical information, respecting all the operations of the Creator in times and places with which the human race has no concern ..."
>
> (Buckland 1836, p.14)

Buckland's second major work (the *Bridgewater Treatise on geology and mineralogy*, 1836) was immensely influential, both in Britain and in continental Europe through its translation by Agassiz (Rudwick 1972: 203). This later view of the origin of the fossil cave faunas and their impact on the Mosaic account of creation was also held by many of Buckland's contemporaries, both ecclesiastical and scientific (see Rudwick 1972: 168–172). But they were opposed strongly by others. Public awareness was torn between authorities who, both churchmen and scientists, were challenging the simplistic biblical literalism that was the comfortable faith of the educated public (and of many, if not the majority, of the clergy).

From Mitchell's correspondence with his friend George Ranken (in Ranken 1916) it is clear that these issues motivated him. Certainly the anonymous 'L' (Anon. 1830b), had published in Sydney his Diluvial interpretation of the Wellington fossils before Mitchell entered the caves. Even before the Wellington discovery, Mitchell had searched caves at Bungonia (Fig. 4) for bones (Holland 1992), and this enthusiasm for the search for fossil bones permeates his writing. The words of his description (1838, vol. 2) of Ranken's discovery are as vivid today as when they were written.

Figure 4. Locality map showing vertebrate fossil localities mentioned in the text.

> "The pit had been first entered only a short time before I examined it, by Mr Rankin [sic.], to whose assistance in these researches I am much indebted. He went down by means of a rope, to one landing place, and then fixing the rope to what seemed a projecting portion of rock, he let himself down to another stage, where he discovered, on the fragment giving way, that the rope had been fastened to a very large bone and thus these fossils were discovered." (p. 362)

Mitchell was determined to extend his discoveries and, having seen for himself the circumstances under which the cave fossils occurred, and having learned of the existence of other caves in the vicinity of Buree (Borenore), he and Ranken went to look for yet more bones. So riding along Oakey Creek

> "We soon found one, which I considered to be of the right sort, viz. a perpendicular crevice with red tuff about the sides. Being provided with candles and ropes, we descended perpendicularly first, about six fathoms to one stage, then obliquely, about half as far to a sort of floor of red earth; Mr Rankin [sic.], although a large man, always leading the way into the smallest openings. By these means, and by crawling through narrow crevices, we penetrated to several recesses, until Mr Rankin found some masses of osseous breccia beneath the limestone rock…" (p. 7)

Shortly after the initial discoveries at Wellington, which stirred scientific interest in Europe (and seem to have contributed to Buckland's change of mind over the Diluvial age of cave fossils, see Mitchell in Ranken 1916), exploration northwards by

Mitchell and others, and pastoral and agricultural expansion, led to the finding of the prolifically bone-bearing alluvial deposits of the Condamine River and its associated streams and in turn to a steady flow of material to European scientists (and particularly to the young and energetic Richard Owen, at the Royal College of Surgeons, who was then building his reputation as the "British Cuvier", see Owen 1894, MacLeod 1965, Rupke 1994).

It was not long before many other caves and alluvial deposits became known throughout eastern Australia from the Darling Downs to western Victoria (Owen 1858). In extending these discoveries, the interest of Dr George Bennett (see Bennett 1834 1: 226 — description of Goodradigby Caves) and the early development of the Colonial Museum, in which he was closely involved (Strahan 1979), played an important part and which, together with the direct role later played by the able and turbulent Gerard Krefft, laid the foundations of indigenous mammal palaeontology.

From the very beginning of Owen's involvement by Mitchell in the Wellington Cave fossils, Owen made the Australian fossils very much his province and this interest continued throughout his life resulting in both the publication of numerous papers and his monumental *Researches on the fossil remains of the extinct mammals of Australia* (Owen 1877). He also persuaded the New South Wales Colonial Government to fund exploration of the Wellington Caves by Gerard Krefft and Professor A.M. Thomson in 1867 (New South Wales, Parliamentary Papers 1870, Owen 1877: 239–40).

We make no apologies for dwelling on this aspect of the role played by the "philosophical" issues motivating the beginnings of cave palaeontology in Australia, because it explains both why and how these early players could create, from the outset, the interest and support that they received both within the Colony and in Europe; but it must not be thought from it that people like Mitchell, Owen and Bennett were not also driven to enquiry by scientific curiosity.

If we look at the results of their researches — and their conjectures — we see that almost all the questions that we are asking of our material today are questions that they were also asking 160 years ago.

In their writings we find that they were moved by curiosity about taxonomy, anatomy, biogeography, extinction, evolution, stratigraphy, dating, palaeoclimatology, and landscape evolution. And at that time, most such questions could find no answers — only conjecture, nevertheless they were being asked.

We will also find, as we do today, that their conclusions and conjectures, themselves, motivated challenge by others. So that now, at a time when the "philosophical" issues of the mid-19th Century produce little more than a yawn, except among dogma-driven creationists, other philosophies have taken over the scientific mind (such as environmental sustainability, biodiversity, and cladism). But to most of us the forces that drive our curiosity remain the same basic scientific questions — being asked with more sophistication and being answered from a perspective of a century and a half of accumulated knowledge, and with greater technical capacity than our predecessors had.

Taxonomy and anatomy

It is of no surprise that most of the early interest in the Pleistocene faunas was anatomical and taxonomic (in the sense that their relationships with the fauna of the known world had to be clarified and described).

In the early period, anatomical interpretation and relationships were argued and established by such people as Pentland, Owen and Clift, and later, in Britain, by Huxley and Flower, and by Krefft in Australia. Thus, initially, there was debate as to whether *Diprotodon* had been hippopotamus, dugong or elephant (see Mitchell 1843 MS., published in Mahoney and Ride 1975: 222–3). And once its marsupial status established, whether it was syndactyl like other diprotodonts.

The debate that followed the discovery in 1846 of the first remains of *Thylacoleo* raised issues about its carnivory — an issue only recently settled beyond dispute (Finch

1982, Wells et al. 1982). Owen, in philosophical mode four years before, in 1842, had argued that among so many large herbivores there must also be a large carnivore to control their populations (Owen 1858). From slender material, he diagnosed the newly discovered remains as marsupial, dasyurid and, on functional "Cuvierian" grounds, carnivorous. Subsequent discoveries revealed its diprotodonty and an argument against the "carnivorous hypothesis" was generated in opposition (in this Owen's principal opponents were Flower and Krefft who argued primarily from the taxonomic grounds that a diprotodont marsupial could not be a carnivore).

Even today, this area of debate continues over similar questions in connection with the morphology of *Palorchestes* and *Propleopus* (see Ride et al. this volume).

Biogeography and evolution

But biogeographical and evolutionary implications were seen even at this early stage. Thus, as mentioned already, in 1833 Mitchell wrote to Ranken and mentioned the effect that the Australian bones were having on Buckland's expectation that they would be of hyaenas and cave bears.

Jameson (1831) had drawn attention to the fact that it follows from the Wellington fossils "That New Holland was, at a former period, distinguished from the other parts of the world, by the same peculiarities in the organisation of its animals, which so strikingly characterize it at the present day." (p. 395). In 1833 Lyell drew attention to the same phenomenon. He commented in *The Principles of Geology* that "These facts are full of interest; for they prove that the peculiar type of organization that now characterises the marsupial tribes has prevailed from a remote period in Australia ..." (p. 144).

Not only did these discoveries lead Owen and others to challenge the view held on literalist scriptural grounds that the "post-Diluvian" faunas must have originated from a single centre of dispersal in Asia, but led both Darwin (as one of the results of his voyage in the Beagle between 1831 and 1836) and Owen, (who received Darwin's South American Pleistocene fossils in 1835, the year after he received a second collection of Wellington Caves fossils from Mitchell), to enunciate the "laws" of animal distribution that Darwin (1839) called "the law of succession of types" and Owen (1845) a "law of distribution of extinct Mammalia" (and later (Owen 1858) the "law of succession of organizational types"). Moreover, it led them both, inexorably, to their separate and different convictions that species had a natural origin (Dugan 1980; Rupke 1994, p. 220, 223–225).

Despite the fact that possible mechanisms of evolution were under discussion well before the time of the discovery of the Wellington fossils, that the concept of progressive geological change was well accepted, and that it was recognized that proofs of progressive and directional change in organisms must be looked for in the fossil record, there seems to have been no early attempt to interpret the Australian fossils in evolutionary terms.

The Australian cave faunas contained both unknown species and many that appeared to be close to modern forms. Among these were some which, although recognized as distinct species, were much larger than their modern counterparts (e.g. *Thylacinus, Sarcophilus*, and *Macropus*). Yet at that time no one seems to have regarded them as evolutionary forerunners and it is only in modern times that the question of "dwarfing" has been raised (e.g., Marshall 1973, Marshall and Corruccini 1978, Dawson 1985). Instead, they were regarded in the same way as the "Ice Age" mammoths and cave bears of European caves had come to be regarded once the "diluvial debate" was over, namely to represent an antique fauna which had become extinct[2] in the last cycle of extinctions and replaced by the modern fauna.

However, it was not long before the evolutionary debate was fuelled in the public arena by the publication of the *Origin of Species*, and natural selection proposed as its cause. Fossil evidence in support of gradual evolutionary change soon followed in Gaudrey's demonstration in 1866 of gradual horse evolution in deposits from Pikermi in Greece; in 1868 Huxley demonstrated the presence in the fossil record of intermediates between classes in *Compsognathus* (a "bird-like reptile") and *Archaeopteryx* (a "reptile-like bird") (see Rudwick 1972: 245–252). It then became only a matter of time before Australian fossil mammals were being described and studied in those terms. Thus, in 1888, De Vis in describing *Triclis oscillans (*i.e., *Propleopus)*, suggested that *Hypsiprymnodon* could be "a continuation of a stock" (the "Propleopodidae") "whence has arisen the Phalangistidae [Phalangeridae] on the one hand, the Hypsiprymnidae [Macropodidae] on the other" (De Vis 1888: 8). Shortly afterwards in 1896, Robert Broom in describing the fossil mammals of the Wombeyan fauna, remarked of *Burramys parvus* that "On the whole it would seem that we have in *Burramys* one more link in the chain binding the Kangaroos and Phalangers. The main links would thus be — *Macropus, Aepyprymnus, Hypsiprymnodon, Burramys*" (Broom 1896a), and of *Palaeopetaurus elegans* that "In many respects it stands intermediate between the two genera [*Gymnobelideus* and *Petaurus*], and not improbably may be the common ancestor of both" (Broom 1896b).

Dating the bones

Mitchell and others were not able to suggest any particular age for the faunas from Wellington and Borenore. In the light of his observations Mitchell did not see anything "likely to throw any light on the history or age of the breccia, but the phenomena they present seem to indicate more than one change in the physical outline of the adjacent regions, and probably of more distant portions of Australia, at a period antecedent to the existing strata of the country".

Today, dating (together with a lack of stratigraphic understanding) remains the single most pressing impediment to the interpretation of the cave faunas.

Palaeoclimatic framework and landscape evolution

Mitchell speculated that the position of the breccia in Wellington Caves, and other caves, indicated that the bone breccia formed during a long dry period between two more humid periods. He reasoned that during these humid periods sea levels would have been higher and inland Australia inundated (Mitchell 1838, vol 2: 370 et seq). He argued that the lunettes on the north-eastern shores of inland lakes that he had discovered in the Wimmera, and the grassy plains between the lunettes and the lakes, supported this conclusion; he also correlated the periods of inundation with the period of lunette formation (p. 373).

From the fact that the bone breccias occurred also as surface outcrops exposed by erosion, he concluded that their exposure had occurred as new drainage formed on the slopes following the most recent retreat of the water body (Mitchell 1838, p. 371). Even today the age of these cave breccias exposed on the surface, and the time required for their exposure, remain problems (Osborne 1992).

Richard Owen reached a different palaeoclimatic conclusion from that of Mitchell. He considered that the fauna accumulated under wetter conditions than at present — not drier. He argued that the bulk and similarity of the megafaunal marsupials to such forms as the elephant and hippopotamus indicated a luxuriantly vegetated environment.

That conclusion was shared widely and led to general acceptance that megafaunal extinction resulted from the subsequent aridity. Darwin dissented (Darwin 1845, p. 98). He pointed out that modern savannah megafauna in Africa occurs abundantly in arid environments. Nowadays it is recognized that megafaunal bulk may confer physiological advantages in situations where dietary nitrogen and energy are low, but under those conditions may also be disadvantageous unless cool refuges (shade) or ample water for evaporative cooling are available (Main 1978). In short, the Australian megafauna occurred under a wide range of climatic conditions but individual species (e.g. *Diprotodon optatum, Zygomaturus trilobus)* may have responded in different ways (Hope 1982).

THE SETTING

Today, our palaeontology is conducted within a very different framework of knowledge of geology, the timing of events, and palaeoclimatology which, if we are palaeozoologists (as we are) is derived from outside our field. This framework of knowledge provides not only an environmental and temporal structure to which our observations can relate, but it also provides a control on our speculations. No longer do we look to the fossils to provide proofs of evolution, or (except in cases where there is no modern survivor) of relationships of major groups. Instead, we look to the fossils to fill in the gaps (both taxonomically and structurally), to fill out our knowledge of past radiations and palaeobiogeography, to provide their own comments on environmental change, and to exercise controls on hypotheses of the timing of evolutionary events based on biomolecular constructs.

But within that new framework, the questions that Mitchell posed in 1838 about wider issues remain cogent.

Geology and landscape evolution

With our knowledge of the evolution of the Eastern Highlands and their cave systems (e.g. Osborne and Branagan 1988) we now recognize temporal complexity, and in particular that their fossils may represent faunas and their evolution over a period far greater than the Quaternary.

The prolific occurrence of caves and their variety are the result of the events that produced extensive sequences of weathering limestone rocks along the Eastern Highlands that are the product of uplift and subsequent continuous weathering.

The highlands owe their origin to a swelling in the mantle that occurred along an approximately meridional line during the Cretaceous (at some time between 96 and 84 Ma (Veevers et al. 1991, figs 6, 7) commencing the development of the sea floor spreading episode that opened the Tasman Sea and continued through with slow spreading until about 55.5 Ma (Veevers et al. 1991, fig. 9). The western side of the ridge that developed, in consequence, is represented by the elevated eastern side of the continent as it is today and crosses all the old geological boundaries from south to north resulting in exposure of a variety of basement rocks including extensive sequences of limestones.

In New South Wales the sequence from south to north is as follows (Packham et al. 1969): The basement rocks of the Southern Highlands are Cambrian–Late Devonian in age, mostly either marine sediments or igneous rocks; they are intruded by granites of Ordovician–Carboniferous age. Northwards the basement rocks of the Hunter Valley are marine shallow water sediments and coal measures of Permian age, overlain by fresh water Triassic sediments. The basement rocks of the New England Tableland are Devonian–Permian in age and consist mainly of sediments and volcanics laid down offshore; they have been intruded by granites of Permian–?Traissic age.

Between 96 and 84 Ma , northward movement of the Australian plate commenced (Veevers et al. 1991, figs 6 and 7), accelerated during the Tertiary (Veevers et al. 1991, figs 9–14), and has continued to the present. As it did so, eastern Australia moved over hotspots in the mantle with the result that volcanic flows penetrated the surface during the Tertiary and Quaternary. Some were very extensive (Duncan and McDougall 1989). The New England, Monaro, and Victorian Highlands basalts piled up great thicknesses (Voisey 1969, Wilkinson 1969, Knutson and Brown 1989, Day 1989), thus increasing the height of the highlands.

The significance of these events to the Tertiary and Quaternary palaeontology of cave and fissure fills lies in the development of karst in the uplifted limestones and its timing. Extensive caves and fissures developed and filled possibly in the Late Cretaceous and probably through much of the Tertiary and up to the present day (Osborne 1992, 1993); some speleogenesis resulted from altered drainages from basalt fills in the valleys (Osborne 1986).

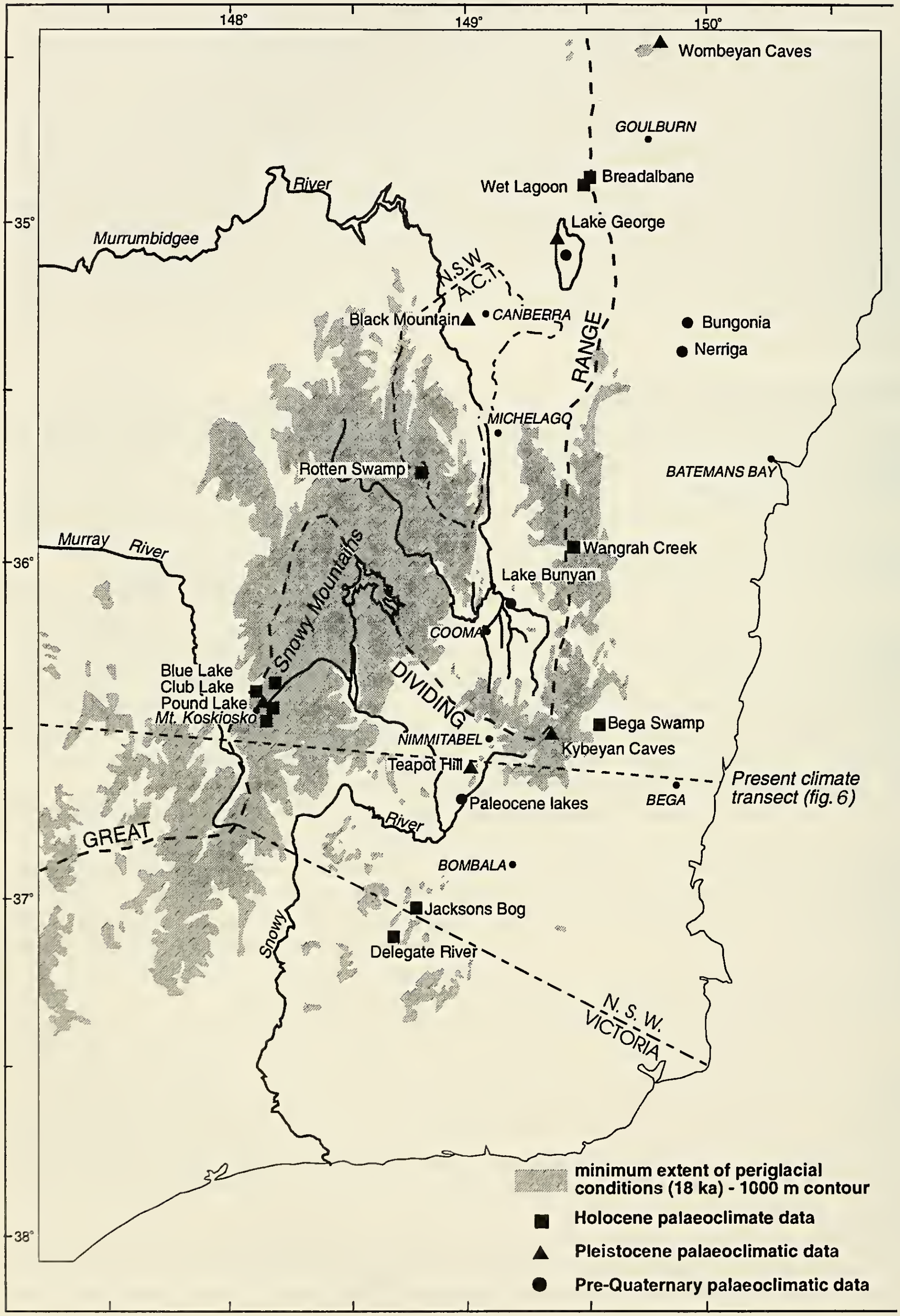

Figure 5. Localities of palaeoclimatic data in the Southern Highlands.

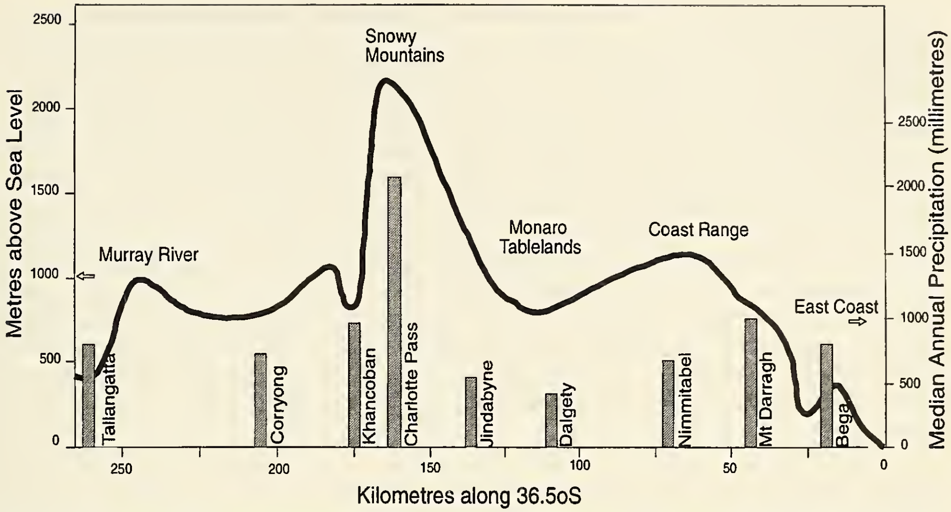

Figure 6. Elevation and annual precipitation across the Monaro Tablelands indicating the rainshadow in the lee of the Snowy Mountains (modified from Atlas of Australian Resources 1986). Median annual precipitation (mm.) at Western Plains, N.S.W. localities comparable with Dalgety (410) is Nyngan (411), Condobolin (423), Leeton (430), Forbes (487) (data from Bureau of Meteorology, 1988, Climatic Averages Australia, A.G.P.S. Canberra).

These events are important in understanding other fossil sites as well. The extrusion of Tertiary and Quaternary basalts over an old landscape covered fluviatile and lacustrine deposits in both the Mesozoic and Tertiary erosional surfaces (Vallance et al. 1969, Pratt et al. 1993). Mammal-containing deposits in the deep leads at Gulgong and at the nearby Canadian Lead (see Woodburne et al. 1985) are good examples from the Eastern Highlands. The basalt flows filling deep-lead valleys on the Gulgong Surface average 14.3 Ma in age; the valley gravels were buried beneath basalt flows in middle Miocene times (Dulhunty 1971).

Because of their weathering and calcium richness, many of the basalts produced conditions in channel fills and terraces favourable to the preservation of bone — as we find in the Monaro.

Finally, as the present landscape formed during the climatic changes and as the uplift continued, river and lake deposits accumulated in the valleys and flood plains from the detritus produced by weathering the exposed highlands. Examples are seen in the valleys of the Bow River and the McLaughlin River where terraces containing mammal fossils extend from the Tertiary to the present, and in the Quaternary sequences of the Monaro (such as at Pilot Creek, Davis 1996).

Palaeoclimatic framework

A general framework of the sequence of palaeoclimatic changes during the Quaternary (and in particular for the Late Pleistocene (120 ka–10 ka), and Holocene) is now available for eastern Australia including the Eastern Highlands of New South Wales.

This part of the palaeoclimatic record is primarily derived from pollen records from a large number of sites, including sites in the Eastern Highlands (see Fig. 5). A few sequences extend back before the last glacial cooling (35 ka–15 ka), and one (Lake George) to before 350 ka, containing evidence of at least four glacial periods (Singh and Geissler 1985, McEwen Mason 1991). Other evidence of climatic change in the period comes from direct evidence of glacial and periglacial features (which in Tasmania provides evidence of 3 glaciations), sedimentology (including evidence from the Riverina, which reflects activity of the adjacent catchment), and the palaeoecology of aquatic non-marine invertebrates (such as ostracods).

Although lacking the detail of modern deep-sea records of the same period derived from isotope studies, and allowing for the fact that parts of the interpretation are probably influenced by local topographic factors, the general sequence of events in the terrestrial climatic framework accords well with the oceanic record (for comprehensive palaeoclimatic summaries see Chappell 1991, Truswell 1993, Hill 1994, Kershaw 1995).

While the environmental consequences of this sequence are a major factor to be considered in interpreting observed differences between faunas, in the context of highland faunas, local palaeoenvironmental variation at any one time must also be expected to have had marked consequences — even over very short distances.

Today altitudinal variation (topography and erosion surfaces resulting from uplift), aspect, geology, soils, and the availability of surface waters from run-off, all have local effects. For instance, in the Monaro, the local effect of a rainshadow in the lee of the Australian Alps results in environments in the Tableland as arid as those in the western plains of New South Wales (see Fig. 6), yet, despite the aridity, the country is well watered by such rivers as the Murrumbidgee and the Snowy, fed by run-off from the adjacent mountains.

These factors combine to produce environments unique to eastern Australia, such as the alpine zone, as well as a varied and disjunct patchwork of mesophyllic and xeric habitats.

There is good evidence that, even in the Tertiary and Quaternary, this environmental patchiness existed even to the extent that the Monaro rainshadow existed in the Miocene (Ride et al. 1989). The consequence has been that during extremes of aridity in adjacent southern and central Australia the highlands were potential refugia for a wide range of differently adapted mammals that must be expected to occur in contemporary deposits.

As Hope (1982) has pointed out, proximity of arid to well-watered environments has enabled the unexpected, and apparently disharmonious, sympatry of some species in deposits, such as those at Wellington, of forms such as *Diprotodon* and *Zygomaturus* that appear from their distributions to be otherwise ecologically incompatible. In places where environmental patchiness is represented within the hunting ranges of predators inhabiting a cave (such as owls) mixed "pseudosympatry" may be expected in a deposit.

As well as resulting in environmental patchiness, altitudinal variety also has direct consequences to faunal evolution and movement over time. It may result in distributional disjunctions. Thus, populations dependent upon alpine habitats (such as populations of *Burramys parvus)* become isolated as temperatures rise, and become reunited with falling temperatures. The drowning of Bass Strait at the end of the Pleistocene produced a major disjunction and barrier to faunal dispersal.

Highland caves and small valley systems are extremely sensitive indicators of faunistic change over relatively small time-spans but, in these complex environmental situations, differences between adjacent faunal assemblages may be due to a number of factors, both ecological and chronological. Unless stratigraphic relations are very clear and dates reliable, faunistic and palaeoenvironmental interpretation is hazardous. Extreme caution must be exercised in attributing biostratigraphic conclusions to them, as we have found in the Monaro.

As an example, until six months ago, on the basis of radiocarbon dates, we thought that the Bunyan Siding and Pilot Creek faunas in the northern Monaro (see below) were contemporary. We concluded that the observed difference reflected ecological responses at the two localities. Instead of which, we now find, from improved dating techniques, that they are separated in time by at least 100 ka (or even 750 ka), and by at least one climatic fluctuation. We now regard differences between them as an example of faunal turnover during the Pleistocene.

Interpretive consequences of the palaeoclimatic record

From different sources of information a dramatic shift in Australian climate took place about eight million years ago (see Kershaw et al. 1991, Truswell 1993, Hill 1994). Although Megirian has argued for the presence of mesic, and even xeric, environments across Northern Australia even earlier, in Miocene (Carl Creek Limestone) times (Megirian 1992), a change of climate occurred from non-seasonal and warm humid conditions, probably supporting extensive rainforest faunas (possibly through a period of shrinking refugia), towards conditions that by five million years ago had become arid and seasonal (Bowler 1982). Moreover, over much of Australia the seasonality of rainfall shifted from summer to winter. During this shift, except in patchy remnants, vegetation became dominated by sclerophyll and other arid adapted plants such as grasses, acacias and chenopods. Yet in the highlands where mesic environments persisted (Hill 1994), traces continued to survive, in wet sclerophyll, in heaths, and downslope in coastal scrubs, of the humid adapted elements of the late Pliocene mammal fauna (such as the ring-tail possums and *Burramys*) which we know from the transitional period at about 4.5 Ma (Hamilton, Bow, and Chinchilla), as well as in much earlier Tertiary faunas (Riversleigh).

The palaeoclimatic record also indicates that in the last two million years there were 20 marked climatic shifts (Chappell and Shackleton 1986, Hope 1994). There is terrestrial evidence that at least three of these resulted in glaciations (Colhoun 1985). At the height of these the arid threshold was passed, sand deserts formed and dune building occurred (Wasson 1986, Hope 1994). Major expansion of dunes occurred after 700 ka.

The most striking characteristic of the modern Australian mammal fauna is its remarkable adaptation (anatomical, physiological and behavioural) to aridity and climatic instability. From the palaeoclimatic sequence outlined above, it is now apparent that this adjustment must have generated an extremely rapid faunistic response over much of Australia; and that there was a succession of extinctions culminating in the final extinction of the remaining megafauna. The whole sequence, from the start of the aridity to the present day, taking little more than five million years.

As a late Tertiary and Quaternary phenomenon this period of adaptation to arid and semi-arid conditions (by evolution and by faunal movement), probably took place within the time span covered by the eastern highland deposits and, because of this, these deposits should, once we are able to determine their stratigraphy and date them, provide us with a remarkably detailed record of it.

At present there are few data of eastern Australian cave mammal faunas that can be securely positioned within the palaeoclimatic record until we reach the end of the penultimate interstadial at about 30 ka (and even then, records are inadequate).

Of lower- to mid-Pleistocene eastern highland faunas, only Bunyan Siding is securely dated to this period (i.e., to more than 100 and less than 780 ka). Dawson (1985) has argued that part of the Wellington Cave deposit (the Phosphate Mine Beds and Big Sink) is late Pliocene. On the basis of the contained macropod species, she has also argued that the bones in the Wellington red earths (Bone Cave, Mitchell's Cave) may be as old as 128 ka (also see Osborne 1983, p. 143–4, for an evaluation of studies bearing on the ages of these units at Wellington).

In support of Dawson's contention that the Wellington red cave earths may be older than the last glacial cycle, on faunistic grounds alone, there can be no doubt that the Wellington Caves deposits cover a number of replacing faunas. At least 27 species of Macropodidae are represented in historic collections from the caves. By comparison, the richest modern fauna of Macropodidae recorded (that of the Upper Richmond and Clarence Rivers — Calaby 1966) contains 11 species — and even that occurs over a very diverse catchment of some 4000 km^2. Bunyan Siding, that we assume contains a single fauna, contains at least 7 species of Macropodidae.

Of earlier deposits, there is now no doubt that Dukes cave system at Buchan contains bone bearing deposits formed in a period of magnetic reversal. These are at least older than the end of the Matuyama chron which finished 0.73 Ma ago (Osborne 1983, Webb et al. 1992, Cande and Kent 1992), but nothing is yet known of the fauna.

As the climate of the eastern highlands moved towards the last glaciation after about 30 ka, it changed from cool temperate and moist interstadial conditions, through increasing aridity and reduced temperatures until the glacial maximum was reached at about 18 ka when temperatures were probably about 9 C below the present (Barrows 1995).

The glacial maximum was followed by climatic amelioration with increased humidity and a temperature that at 6 ka probably reached about 1–2 C above the present. From then until the present, temperatures fell again and it became slightly more arid (Kershaw 1995).

Many of the morphological changes in animals, and changes in species composition, particularly those brought about by gradual responses to changing climates, will be expressed only by changes in ranges of variation, and abundance of species, and will only be detected statistically and as a result of detailed quantitative and stratigraphic study. Some cave deposits are ideal for this and a fine example is provided by the detailed study made by Deborah Morris and colleagues (Morris 1992, Morris et al. 1996) at Jenolan. In other parts of Australia similar studies have been made by Alex Baynes at Hastings Cave in Western Australia (Baynes 1979), and are currently being made by Rod Wells and his colleagues at Naracoorte.

As collections made in former times from caves at Wellington attest, collections made before the need for rigorous localization was recognized, present almost insuperable difficulties in interpretation (see Dawson 1985).

Dated mammal-containing sites from the period of maximum aridity (i.e. immediately before and after the last glacial maximum) are known from throughout the region. In the southern highlands, as well as those we have dated in the Monaro, dated deposits occur at Lake George (21–27 ka, Sanson et al. 1980) and at Cloggs Cave, Buchan (17–25 ka, Flood 1974, 1980), and Pyramids Cave, Buchan (33–30 ka, Wakefield given in Flood. 1980); and in northern New South Wales at Lime Springs, Gunnedah (20–18 ka, Gorecki et al. 1984).

Dated deposits from the north and south of the region also indicate changes in mammal faunas over this time. The southernmost dated records are from the Florentine Valley, Tasmania (20–10 ka, Goede and Murray 1979), northwestern Tasmania (Pulbeena Swamp, 22 ka, Banks et al. 1976) and Hunter Island (Cave Bay Cave, 23–14 ka, Bowdler 1975). From southern Victoria, dated late interglacial deposits from before the last glacial maximum are Lancefield (c 26 ka, Gillespie et al., 1978), and Spring Creek (>30 ka. White and Flannery 1995). In southern Queensland a dated deposit is known in the western Darling Downs at Kings Creek, Clifton (over 21 ka, Gill 1978).

Of these series, Baynes (1995; pers. comm.) considers that only the dates from Cloggs Cave. Buchan; Kings Creek, Clifton; and the Lancefield Channel have values of 8 or more in the Meltzer and Mead (1985) classification (i.e. can be considered reliable). But in the case of the Lancefield Channel, there is subsequent indication that the fossils within the site have been redeposited (Van Huet 1994). Baynes has not commented on the date given on Pyramids Cave (in Flood 1980), while our most recent dates for the Bunyan Siding and Pilot Creek deposits were obtained after his survey and have not been commented on, either.

Dated mammal-containing deposits from the post-glacial period of climatic amelioration, including the warm moist phase of the early Holocene, are less abundant. In the Eastern Highlands dates have been obtained from Nettle Cave, Jenolan (7.1 and 8.7 ka, Morris 1992) and by us for Coronation Cave, Wombeyan (8.2 ka — but we do not consider this date reliable for the contained fauna). We have also dated post-glacial sediments in the Monaro (Davis 1996).

Southwards, post-glacial dates are known for mammal-containing deposits at Cave

Bay Cave, Hunter Island (c.7 ka, Bowdler 1975), Pyramid Cave, Buchan (c.2.5 ka, Wakefield 1967a), and numerous archaeological sites containing mammal remains such as Capertee Valley (with a dated succession from 7.4 ka–2.9 ka) and Burrill Lake (younger than 1.6 ka). Some dated faunas from this later period are parts of sequences from which the dates of older parts of the same sequences can be inferred. These include Pryamids Cave, Buchan (2.5 ka, Wakefield 1967a) and McEachern's Cave in Western Victoria (15 ka, Wakefield 1967b).

REFLECTIONS: ON CURRENT DIRECTIONS

Stratigraphic correlations of open sites

The temporal and palaeoclimatic setting described above has given new possibilities to Quaternary mammal palaeontology. Providing dates can be obtained it should now be possible to correlate palaeoclimatic events and faunal changes such as faunal turnover, extinction, or morphological changes and give ecological meanings to them.

Woodburne et al. (1985), in their survey of the biochronology of the continental mammal record of Australia and New Guinea, point out that, as the result of correlating late Tertiary and Pleistocene faunas of arid Australia with such events as dune building, we know that major faunal changes have taken place during the Quaternary and not only at its end. They say

> "In addition, certain Tertiary groups (for example, diverse diprotodontines) fail to persist into late Pleistocene time and give evidence of important faunal change within the Quaternary that needs better documentation. Integrated palaeontological and geological studies are badly needed to chart the Quaternary faunal changes and determine their causes against the background of Australia's unusual Pleistocene history."
>
> (Woodburne et al. 1985, p. 360)

In the Eastern Highlands numbers of open sites (i.e. sites accumulated under fluviatile or lacustrine conditions) containing mammals have been described. Jeanette Hope (MS. pers. comm.) and Paul Willis (MS. pers. comm.) have listed these from thorough surveys of the literature and museum collections. Most of these sites, with further work, have the potential to be placed within the framework but none, except those we have studied in the Monaro and the Governors Hill site, are dated. We conclude that, in the absence of dates, attempts to incorporate them in a general biostratigraphy of the region would be hazardous. Of relevant sites to the northwards, Bingara, of which the fauna was revised by Marcus (1976), is the richest and has great potential for further study. Weetaliba, which we have surveyed, although rich in numbers of species represented, is very dispersed and appears to lack concentrations of fossils, and we have not found it to have potential for dating.

Over the last 10 years we, with Leanne Dansie (now Armand), Prof. Graham Taylor and Dr Pat Walker, have investigated three alluvial Quaternary sites in the Monaro (Dansie 1992, Davis 1996). Faunistically, our aim was to clarify what happened to the high country faunas in eastern Australia during the decline of the megafauna. We have attempted to find causes by seeking correlations with other factors, such as the palaeoclimatic events that have been revealed by studies from other disciplines.

The sites studied are Bunyan Siding and Pilot Creek, both on tributaries of the Murrumbidgee River near Cooma, and Teapot Creek, a tributary of the Maclaughlin River near Nimmitabel. At Bunyan Siding there are two faunas, both now considered to be Middle Pleistocene. Pilot Creek provides a record of the last 25 ka represented in four stratigraphically distinct faunas with radiocarbon ages of 25, 11, 6 to 2, and 4.5 ka. At Teapot Creek there are two faunas, the younger dated at 4.5 ka and the other which occurs in a series of terraces is yet undated and is, from the species represented, probably

Pleistocene. At the Maclaughlin River, close by, a fauna contains species apparently equivalent to Pliocene Chinchilla. Between them, these sequences in the Monaro give a picture of faunal turnover between the Middle and Late Pleistocene (and possibly the late Pliocene), followed by progressive faunal impoverishment since immediately before the last glacial maximum to the present.

The Middle Pleistocene fauna of Bunyan Siding contains at least 17 species of mammal (11 extinct, 6 extant). Of the 11 extinct, 7 are Macropodidae (i.e. as in Wellington faunas (Dawson 1985), all Bunyan Macropodidae are replaced). The other four species are possibly *Zygomaturus trilobus*, a species of *Diprotodon*, a new vombatid, and a small murid of the *Pseudomys australis*-group. The 6 extant species are *Aepyprymnus rufescens, Vombatus ursinus, Perameles gunnii, Dasyurus viverrinus, Ornithorhynchus anatinus* and *Mastacomys fuscus* (Davis 1996).

The older (25 ka) fauna of Pilot Creek, from immediately prior to the last glaciation, contains both modern species such as *Macropus robustus* and *Vombatus ursinus* as well as large megafaunal species (*Protemnodon anak, Protemnodon roechus/brehus, Thylacoleo carnifex, Sarcophilus laniarius, M. titan*, and species of *Sthenurus* and *Diprotodon*) that are not present in the younger deposits. The post-glacial deposits contain no megafauna, but do contain species that are not found in the modern fauna of the area, although occurring elsewhere. These are *Aepyprymnus rufescens, Perameles gunnii* and *Mastacomys fuscus.* Extinct species represented in these post-glacial faunas include *Thylacinus cynocephalus* and *Conilurus albipes.*

It is instructive to compare the result at Pilot Creek with that obtained by Deborah Morris at Nettle Cave, Jenolan (Morris et al. 1996), and that of Norman Wakefield at Pyramids Cave, Buchan (Wakefield 1967a, tables 1 and 2). In both cases they obtained a distinct faunal transition that probably represents the same climatic event but, unlike the megafauna, in the case of the faunas of small mammals that they describe, while clearly there has been an ecological shift, there have been no extinctions.

Did the megafauna have nowhere to go as the climate warmed and conditions improved, or was there some factor other than climate involved. We now have evidence from Bunyan that species had been lost earlier than the last glacial maximum, and local extinction both before and after the last glacial maximum involved more than the megafauna. Certainly, humans had occupied the highlands by 21 ka and maybe long before. The Lake George core has been interpreted as giving evidence of a human-caused increase in burning from before 100 ka (but this interpretation is not accepted universally (Wright 1986, Ladd 1988).

Through the very small window we now have in Bunyan Siding and Pilot Creek, it is possible to see that considerable faunal change occurred between the time represented by Bunyan (somewhere between 780 and 100 ka) and the colder conditions that immediately preceded the glacial maximum represented at Pilot Creek and, probably, Teapot Creek. Of the 41 species of megafauna known from Australian deposits considered to be Pleistocene (Flannery 1990), only 16 occur in deposits known with reasonable certainty to be late Pleistocene (i.e., 25 ka or younger). Have we enough information yet to suggest that only the very end of megafaunal extinction was coincident with a major adverse climate change, and that it may well have commenced before Aboriginal settlement?

Even Owen, in his time, was asking that question.

> In the extinction of Diprotodon, as of Megatherium, there seems to be an additional exemplification of the fruitful and instructive principle which, under the phrases "contest for existence", or "battle of life", embodies the several circumstances , such as seasonal extremes, generative power, introduction of enemies, &c., under the influence of which a large and conspicuous quadruped is starved out, or falls a prey, while the smaller ones migrate, multiply, conceal themselves, and escape.
>
> We infer from the fact of remains of young and inexperienced Diprotodons occur-

> ring in Australian Caverns with those of Thylacoleo, that the large Marsupial herbivore had its enemy in, and occasionally fell a victim to, the large Marsupial Carnivore; as at the present day the Kangaroo is laid in wait for by the Thylacyne, or "Native Wolf", and by the Dasyure, or "Native Cat".
>
> We may speculate upon the possible relation of the first introduction of the Human kind into Australia, and of the subsequent insulation of that land from the rest of the Papuan Continent, to the final extinction in the so restricted territory of all the characteristic Mammals which happened to surpass in bulk the still existing, swift-retreating, saltatorial and nocturnal Kangaroos.
>
> (Owen 1877, p. 233)

Impact upon conservation biology

As precise knowledge of the ages and compositions of the faunas increases, we are going to find that there are many faunistic associations that are not explicable on present ecological knowledge. Lundelius (1989, pp 410–411) gives a number of examples from fossil faunas from different parts of Australia.

In Pilot Creek at the Poplars site (4.5 ka) the three bandicoot species *Isoodon obesulus, Perameles nasuta* and *P. gunnii* are sympatric (Davis 1996), assuming that one can discount the possibility that they were collected by a predator from different, but adjacent, habitats. *P. gunnii* occurs nowhere today with *P. nasuta.* The same species association was found by Wakefield (1964, 1967b) in south-eastern Victorian cave faunas.

The three small possums *Burramys parvus, Gymnobelideus leadbeateri* and *Cercartetus lepidus* provide a similar example. All three occur together in the Broom fauna of Wombeyan Caves. Today, these species have widely separate distributions and seem to differ from each other in ecological requirements. On the basis of current knowledge, their presence in a single fauna would be improbable. A similar difficulty is posed by the palaeodistribution of the native mice *Mastacomys fuscus* and *Pseudomys higginsi.*

Burramys parvus, the mountain pygmy possum, is today confined to high altitudes, living principally in periglacial conditions above the tree line. It is confined to a few localities in the Australian Alps in Victoria and New South Wales. Its principal habitat (Mansergh and Scott 1990) is alpine and subalpine *Podocarpus* heathland over periglacial rock screes and boulder fields.

The palaeodistribution of *Burramys* (see Ride et al. 1989, p 105) includes Kandos (undated), Nettle Cave, Jenolan (undated but probably immediately before the last glaciation), Wombeyan (Broom Deposit and Coronation Cave — both undated), Wombeyan Quarry (undated), Tuglow Downs (undated), and Pyramids Cave, Buchan (between 33 and 30 ka). Tertiary species of *Burramys* occurred in rainforest environments in the Miocene (Riversleigh) and Pliocene (Hamilton).

Other mammals in the modern habitat are *Mastacomys fuscus, Antechinus stuartii, A. swainsonii* and *Rattus fuscipes*. These species seem to be less successful than *Burramys* in that habitat and appear to be approaching their ecological limits.

The major food resource of *Burramys* is the Bogong Moth which congregates in that habitat in large numbers during the summer when the possums are building up energy reserves for the winter when the animal enters extended bouts of torpor between May and early September (Mansergh et al. 1990).

Its behaviour, as well as its physiology, is highly specialized. In addition to hibernating, the females maintain territories in the preferred habitat the year round and the males leave in the autumn to return in the following summer. Breeding is highly synchronized and there is one litter only. They give birth to supernumerary young. They have a greater longevity than any other small Australian mammal species and this, combined with very efficient breeding, gives them a very high lifetime fecundity.

This information all indicates that *Burramys parvus* has very narrow environmental tolerances (i.e. is dependant upon periglacial conditions) and that it should be very sensitive to climatic change. Recent BIOCLIM analysis (Bennett et al. 1991) supports this view. On that basis a few degrees rise in temperature should result in its extinction. Yet the palaeoclimatic framework and palaeodistributional records are inconsistent with that contention. Moreover the species did not become extinct despite the climatic amelioration of the Holocene.

Gymnobelideus leadbeateri, Cercartetus lepidus, Mastacomys fuscus and *Pseudomys higginsi*, pose similar problems in connection with rise in temperature (see Lindenmayer et al. 1991, Bennett et al. 1991).

Does this mean that the use of modern distributions and their inferred ecological "drivers" alone, as in BIOCLIM analysis, is not an effective methodology for predicting distributional consequences of global warning? Bennett et al. (1991, p. 9) make an important caveat that interactions between species may give rise to responses to climate change that may vary from those predicted by BIOCLIM. Graham and Lundelius (1984) suggest that an explanation of apparently disharmonious distributions might be that they reflect the distribution of evolutionary interactions.

Does it mean that physiological evolution can proceed much more rapidly than the morphological changes with the consequence that we cannot assume that past behaviour and physiological responses of modern morphospecies are those of their seeming palaeo-representatives?

Or does it mean that our morphotaxonomy is not sufficiently precise to enable us to detect the differences that are reflected in ecological responses?

Certainly, in the case of *Burramys* recent research by Jenni Brammall has shown that in the Quaternary more than one taxonomically distinguishable form is involved in the puzzle (and therefore are, possibly, physiologically distinct).

It may be any of these things, but Brammall's current study of the *Burramys* populations (pers. comm.), suggests that our principal barriers to understanding in this area stem from a taxonomy that has still a long way to go and the lack of dated sites that would enable us to assign species distributions to positions within the palaeoclimatological framework.

We have come far in understanding since fossils were collected from these caves in 1830, but, even 166 years later, we still have far to go …

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The portrait of Professor Sir Richard Owen is published with the permission of the Trustees of the Wellcome Trust (who hold the copyright) and is from the Wellcome Institute Library, London; that of George Ranken is published with the permission of his great granddaughter Mrs Margaret Suttor of Kelloshiel, Hargraves, NSW; and that of Major Sir Thomas Mitchell is published with the permission of the Mitchell Library, State Library of NSW. We are grateful to William Schupbach who selected the portrait of the young Richard Owen for us from the collection of the Wellcome Institute Library, London, that he curates; to Christina S. Wright for locating the portrait of George Ranken; and to Elizabeth Ellis (librarian) and Jennifer Broomhead (copyright and permissions librarian) of the Mitchell Library for locating the portrait of T. Mitchell.

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ENDNOTES

1. A view later echoed by Wilberforce, Bishop of Oxford, in his 1860 review of *The origin of species* in which he gave his view of the proper attitude to scientific truth. Wilberforce said "We have no sympathy with those who object to any facts or alleged facts in nature, or any inference logically deduced from them, because they believe them to contradict what it appears to them is taught by Revelation … To oppose facts in the natural world because they seem to oppose Revelation … is … but another form of the ever-ready feebleminded dishonesty of lying for God …" (Quoted by Lack 1961, p.14).
2. It should not be assumed that the scientists involved had simply left the issue to rest there. The problem of whether extinction, as a natural process, had occurred at all, had featured prominently in the "philosophical debate" over creation (see Rudwick 1972; e.g., pp 105–9, 171–3). For the Australian fauna this aspect became replaced by speculation over causal factors that might also have operated world-wide (e.g. Darwin 1845, p 178) and by the quest to determine whether humans had had a part in Australian megafaunal extinction (Owen 1877, pp 238–240).

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